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Does gravity influence the visual line bisection task?

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Does gravity influence the visual line bisection task?

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A. A. Tarnutzer: conceived of the study, assisted in analyzing the data and in writing of the manuscript.

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ABSTRACT

The visual line bisection task (LBT) is sensitive to perceptual biases of visuospatial attention, showing slight leftward (for horizontal lines) and upward (for vertical lines) errors in healthy subjects. It may be solved in an egocentric or allocentric reference frame and there is no obvious need for graviceptive input. However, for other visual line adjustments, such as the subjective visual vertical, otolith input is integrated. We hypothesized that graviceptive input is incorporated when performing the LBT and predicted reduced accuracy and precision when roll-tilted. Twenty healthy right-handed subjects repetitively bisected earth-horizontal and body-horizontal lines in darkness. Recordings were obtained before, during and after roll-tilt (±45°, ±90°) for 5min each. Additionally, bisections of earth-vertical and oblique lines were obtained in 17 subjects. When roll-tilted ±90° ear-down, bisections of earth-horizontal (i.e., body-vertical) lines were shifted towards the direction of the head ($p<0.001$). However, after correcting for vertical line-bisection errors when upright, shifts disappeared. Bisecting body-horizontal lines while roll-tilted did not cause any shifts. The precision of earth-horizontal line bisections decreased ($p\leq0.006$) when roll-tilted, while no such changes were observed for body-horizontal lines. Regardless of the trial condition and paradigm, the scanning direction of the bisecting cursor (leftward vs. rightward) significantly ($p\leq0.021$) affected line bisections. Our findings reject our hypothesis, and suggest that gravity does not modulate the LBT. Roll-tilt dependent shifts are rather explained by the headward bias when bisecting lines oriented along a body-vertical axis. Increased variability when roll-tilted likely reflects larger variability when bisecting body-vertical than body-horizontal lines.

New and noteworthy

In this study we investigated the potential impact of direction of gravity on visual line bisection tasks. Measuring line bisections either along an earth-horizontal or a body-horizontal axis in 20 subjects, we found no impact of gravity on line bisection errors or trial-to-trial variability. This suggests, that for the current setup, gravity does not influence the line bisection task.

INTRODUCTION

The visual line bisection task (LBT) is a behavioral task initially designed to assess hemianopia (Axenfeld 1894), but is now well-established in the research of visuospatial hemineglect (Burnett-Stuart et al. 1991; Heilman and Valenstein 1979; Schenkenberg et al. 1980). Factors like age, sex, handedness and scanning direction influence the LBT in patients and controls (see (Jewell and McCourt 2000) for review). Neurologically intact participants tend to bisect horizontal lines slightly to the left of the objective center, which is known as left-side underestimation (LSU) or «pseudoneglect» (Bowers and Heilman 1980; Jewell and McCourt 2000). Different mechanisms have been proposed as an explanation for pseudoneglect, such as unilateral hemispheric activation (Bowers and Heilman 1980; Bradshaw et al. 1987) or scanning tendency due to reading habits (Chokron and De Agostini 1995; Chokron and Imbert 1993) or cursor movements (Chokron et al. 1998). With visuospatial attention being identified as a function of the right hemisphere (Mesulam 1981; Sperry 1973), its activation may lead to an overestimation of the left line segment (Bultitude and Aimola Davies 2006; McCourt and Jewell 1999).

Previously, Bradshaw reported reduced pseudoneglect when roll-tilted 90° ear-down compared to upright position, implying a modulatory effect of posture on the LBT (Bradshaw et al. 1985). In patients with left-sided hemineglect a reduction of rightward directional errors when in supine position was reported, demonstrating that manipulating the gravitational input affects neuropsychological disorders of visuo-spatial processing (Pizzamiglio et al. 1995). These observations suggest that changing the angle between the body and the gravity vector may influence how visual lines are bisected both in healthy controls and patients with hemineglect. Such a shift in perceived direction of gravity may be considered a distortion in the representation of external space. When encoding spatial information about an object, several reference frames are used. While an egocentric reference frame represents objects in relation to the body, an allocentric reference frame represents objects in space and independently from the subject’s current position. Whereas some brain areas are activated for both reference frames (Kravitz et al. 2011), separate circuits (Zaehle et al. 2007) and interactions between the different areas have been described (Neggers et al. 2005; Zhou et al. 2012). The visual LBT is thought to be solved in an allocentric or egocentric field of reference (Kerkhoff 2001) and there is no obvious need for graviceptive input to solve this task.

While little is known about the influence of gravity on the LBT, its effect on visuospatial tasks such as the subjective visual vertical (SVV) has been extensively investigated (De Vrijer et al. 2008; Kaptein and Van Gisbergen 2004; Tarnutzer et al. 2009a; Tarnutzer et al. 2010; Van Beuzekom and Van Gisbergen 2000). Awareness of head and trunk position, orientation in space and perception of gravity are the result of a multimodal integration of sensory input from vestibular (utriculus, sacculus, and semicircular canals), somatosensory and visual signals using internal models to generate an estimate of direction of gravity (Angelaki et al. 2009; Barra et al. 2010). The otolith organs are essential for static gravity perception because they are the only direct information source of the gravitoinertial vector (Schoene 1964). The otolith organs and central computational mechanisms are optimized for upright position and an increase of trial-to-trial variability with increasing whole-body-roll has been observed when carrying out SVV tasks (De Vrijer et al. 2008; Mittelstaedt 1983; Schoene and Udo de Haes 1968; Tarnutzer et al. 2009a; Tarnutzer et al. 2009b). Manipulations of the environment, such as obtaining the SVV while roll-tilted under water, have shown that the influence of proprioception on the SVV is minor compared to that of otolith input in healthy human subjects (Graybiel et al. 1968; Jarchow and Mast 1999; Wade 1973). For visual as well as haptic line adjustments along an earth-vertical (gravicentric) axis or a body-longitudinal (egocentric) axis, Tarnutzer and colleagues observed roll-angle-dependent modulations of alignment precision in all conditions (Tarnutzer et al. 2012). The comparable results in the egocentric and gravicentric (i.e., a special case of an allocentric frame) task suggest that the same mechanism is responsible for the increased trial-to-trial variability in roll-tilted positions. Previously, Barnett-Cowen and Harris reported a modulatory influence on whole-body roll orientation when either using a tactile rod or saccadic eye movements to indicate earth-vertical or body-longitudinal axis (Barnett-Cowan and Harris 2008). Haustein reported decreased precision of egocentric visual alignments in 90° ear-down orientations compared with upright (Haustein 1992). Hence all these studies suggest an integration of graviceptive cues even when solving egocentric tasks.

Based on these observations and the previous report of reduced pseudoneglect when roll-tilted 90° ear-down compared to upright position (Bradshaw et al. 1985), we predicted an integration of graviceptive input when performing the LBT, regardless of the necessity of graviceptive input to solve this task. Due to the decrease of otolith effectiveness in roll-tilted positions (Tarnutzer et al. 2009a), we expected the accuracy and precision of the LBT to be reduced when roll-tilted. Furthermore, five minutes of static roll-tilt may result in a post-tilt bias of the LBT, shifting bisections towards the previous roll-tilted position as described for the SVV after five minutes of static whole-body roll-tilt (Tarnutzer et al. 2013).

MATERIALS AND METHODS

Subjects

Twenty healthy human subjects (4 females; mean age±1SD: 29.0±7.9 years; age range: 20-50 years) were studied. Handedness was assessed in all subjects with a 13-item questionnaire (Chapman and Chapman 1987) and only right-handed subjects were included (average score±1SD: 14.0±1.2; right-handedness defined as score between 13 and 18). While gender-specific differences have been described for line bisection tasks (Jewell and McCourt 2000), we did not stratify for gender and did not perform any comparisons since the number of included female participants was small.

Ethics statement

Written informed consent of all subjects was obtained after a full explanation of the experimental procedure. The protocol was approved by the Cantonal ethics committee Zurich and was in accordance with the ethical standards laid down in the 2013 Declaration of Helsinki for research involving human subjects.

Definition of frequently used terms

Adjustment errors refer to the deviations from the objective line midpoint in degrees and express the accuracy (i.e., the degree of veracity) of adjustments. Line bisection errors when bisecting horizontal and oblique lines was defined as positive when deviating to the right and as negative when deviating to the left from the subject's viewpoint. For vertical line bisections, errors had a positive sign when deviating upwards and a negative sign when deviating downwards. The trial-to-trial variability indicates the degree of reproducibility between single adjustments in individual subjects, and was expressed as the standard deviation (SD).

Experimental setting

Subjects were seated upright on a turntable with three servo-controlled motor driven axes (Acutronic, Jona, Switzerland) and were secured with a 5-point safety belt. An individually molded thermoplastic mask (Sinmed, Reeuwijk, The Netherlands) was used to keep the head in an upright and straight-ahead position. Body movements were minimized by placing vacuum cushions between the body and the turntable. At all times, the intersection of the three roll axes of the turntable was centered in the intersection of the interaural and naso-occipital line. Subjects with myopia were allowed to wear their glasses.

A luminous line (length: 470mm, width: 3mm) and its orthogonal intersecting component (length: 35mm, width: 3mm) were generated by a turntable-fixed laser and projected onto the center of a sphere located 1.5m away from the subject's eyes in an otherwise dark environment. This line covered the central 9° of the binocular visual field and allowed subjects to keep gaze straight-ahead while performing the task (Fig. 1A). Turntable accelerations and decelerations were set to $10°/s^2$. A remote control box with a knob and a button was mounted on a safety bar in front of the subject and was used in order to move the cursor (intersecting component) and confirm its position.

/* Figure 1 about here */

Experimental Protocol

Each subject completed two sessions at least half a day apart. During the first session (*paradigm 1*), the line to bisect was always earth-fixed, i.e. earth-horizontal independently of the subject's roll orientation. The line orientation relative to the subject's body-longitudinal axis was therefore changing. During the second session (*paradigm 2*), the line was body-fixed, i.e., always perpendicular to the subject's body-longitudinal axis (=body-horizontal). For both paradigms, recordings before (baseline recordings in upright position), during (±45° and ±90° ear-down positions) and immediately after whole-body roll-tilt were obtained over periods of five minutes each with an inter-trial interval of two seconds, as illustrated in Figure 1B. Trials started five seconds after the turntable came to a full rest after position changes. One block (duration=10min) was composed of the recordings during roll-tilt (5min) and in subsequent upright position (5min). Breaks with the lights turned on were provided after each block.

Additional line bisections in upright position were obtained in bisecting lines along four different orientations (earth-horizontal, earth-vertical, oblique from upper-left to lower-right (ULLR) and from upper-right to lower-left (URLL)) over periods of five minutes in 17 subjects.

Subjects were instructed to rapidly (≤6sec) bisect the line with a short perpendicular cursor as accurately as possible. To achieve the LBT, subjects moved the perpendicular short line left- or rightwards by rotating the knob on the control box clockwise or counter-clockwise. Adjustments were confirmed by pressing a button. The starting position of the bisecting cursor was random. After six seconds the line disappeared and the trial was counted as a miss if not confirmed. The percentage of missed trials was <5% in all subjects.

Data analysis

In each subject and for each five-minute recording period, average errors in line bisection, defined as average shift from the objective center, and trial-to-trial variability were determined and results from the earth-fixed and the body-fixed paradigm were compared. Data points that deviated more than 3SD from the mean (reflecting approximately 0.3% of all data points, or 3-4 trials per subject) were considered as outliers and discarded. Our data was normally distributed (cut-off: $p<0.01$) by the Shapiro-Wilk test for normality, thus statistical analysis was performed using univariate ANOVA (full factorial General Linear Model, SPSS 22.0, Armonk, NY, USA) including Tukey's correction for multiple comparisons. Main effects were scanning direction of the bisecting cursor (n=2; rightward vs. leftward) and turntable position (n=9; baseline upright, roll-tilted (4 conditions) and post-tilt (4 conditions)). Turntable and line orientation signals were processed with programs written in MATLAB™ (MathWorks, Natick, MA, USA). Level of significance was always set to $p<0.05$.

RESULTS

The average number of line bisections within a five-minute recording period was 58.6±7.6. Data from a single subject for line bisections before, during and after roll-tilt are shown in Figure 2.

/* Figure 2 about here */

Effect of scanning direction

The scanning direction of the bisecting cursor had a significant impact on the line bisection error, showing deviations towards the starting direction of the moving cursor. This difference was significant for cursor positions in the earth-fixed (df=1, F=7.364, p=0.007) and the body-fixed paradigm (df=1, F=5.340, p=0.021), while it did not reach the level of significance for trial-to-trial variability neither in the earth-fixed (df=1, F=0.576, p=0.449) nor in the body-fixed (df=1, F=0.701, p=0.403) paradigm. Also, no effect of scanning direction was observed for the error (df=1, F=2.414, p=0.123) and the variability (df=1, F=0.137, p=0.711) for the additional controls in upright position. The overall mean error between rightward (RW) and leftward (LW) cursor movements was 0.07° in the earth-fixed paradigm and 0.05° in the body-fixed paradigm. No significant interactions were found between the direction of rotation and the trial condition for all paradigms (df=8, p>0.05). Therefore, we were able to pool trials independently of the scanning direction and to conduct Turkey-corrected pairwise comparisons in order to detect effects of turntable position.

Paradigm 1: earth-horizontal line bisections

In order to investigate whether line bisection errors and variability modulated with roll-tilt position, we compared results before, during and after 5min of static whole-body roll-tilt. There was a significant main effect of whole-body roll position (df=8, F=6.138, p<0.001). Pairwise comparisons revealed that line bisection errors for 90° right-ear down (RED) differed significantly from 90° left-ear-down (LED) (RW: 0.13±0.37° vs. -0.23±0.25°, LW: 0.22±0.37° vs. -0.15±0.27°, p<0.001). Compared to upright, however, we only observed a significant difference for 90°RED (RW: -0.06±0.16° vs. 0.13±0.37°, LW: -0.03±0.14° vs. 0.22±0.37°, p=0.004). Further significant differences are shown in Figure 3A. Immediately after returning back upright, no post-tilt effect of line bisection errors was found compared to upright baseline for any of the four roll-tilted positions.

Trial-to-trial variability showed a main effect for the trial condition (df=8, F=11.389, p<0.001) with significantly higher variability for all roll-tilted positions compared to baseline (Fig. 3B). For the post-tilt conditions, pairwise comparisons revealed no significant differences in trial-to-trial variability compared to baseline measurements.

/* Figure 3 about here */

Paradigm 2: body-horizontal line bisections

There was no main effect of the trial condition on line bisection errors (Fig. 3C) for the body-fixed paradigm (df=8, F=0.240, p=0.983). Likewise, no post-tilt effect on line bisection errors was noted. Also for trial-to-trial variability (Fig. 3D) no significant main effect of the trial condition was observed (df=8, F=1.458, p=0.172). Lastly, no post-tilt effect on trial-to-trial variability was found either.

Additional controls in upright position

We observed a significant effect of the trial condition on the position of line bisection (df=3, F=4.495, p=0.005) (Fig. 4A). Pairwise comparisons demonstrated a significant difference between average line bisection errors for earth-horizontal and earth-vertical lines (RW: -0.08±0.17° vs. 0.05±0.35°, LW: -0.05±0.13° vs. 0.15±0.34°, p=0.049) and between horizontal and ULLR oblique lines (RW: -0.08±0.17° vs. 0.11±0.26°, LW: -0.05±0.13° vs. 0.19+0.29°, p=0.005), with the latter one deviating slightly right- and downward. ANOVA showed a significant main effect of the trial condition on variability (df=3, F=5.235, p=0.002) and pairwise comparisons demonstrated differences between horizontal and vertical (RW: 0.18±0.05° vs. 0.24±0.09°, LW: 0.19±0.06° vs. 0.25±0.08°, p=0.010), horizontal and ULLR oblique (RW: 0.18±0.05° versus 0.26±0.10°, LW: 0.19±0.06° vs. 0.24±0.09°, p=0.003) and between horizontal and URLL oblique line bisections (RW: 0.18±0.05° vs. 0.24±0.07°, LW: 0.19±0.06° vs. 0.22±0.07°, p=0.039) (Fig. 4B).

/* Figure 4 about here */

Corrected earth-horizontal line bisection paradigm

As detailed in the previous paragraphs, we observed significant whole-body roll-tilt dependent differences in line bisection errors when the line was earth-horizontal. Based on the hypothesis that there may be a bias in bisection secondary to the orientation of the line relative to the body-longitudinal axis rather than the body's orientation relative to gravity, we corrected for offsets in line bisection encountered while upright in individual subjects. Therefore the offset in the vertical line bisection paradigm was subtracted (for 90°LED) or added (for 90°RED), respectively, while the offset from the oblique URLL (for 45°RED) and the oblique ULLR (for 45°LED) paradigm were subtracted. By correcting for these potential offsets (Fig. 5), rightward deviations at 45° LED roll-tilt shifted to slight leftward deviations, while errors at ±90° ear-down positions decreased. ANOVA showed a significant main effect of trial condition on the line bisection error (df=8, F=2.458, p=0.014). Pairwise comparisons (see Figure 4), however, did not demonstrate any significant differences in line bisection between single conditions. The previously significant difference between 90° LED and 90° RED had disappeared (RW: -0.17±0.23° vs. 0.04±0.28°; LW: 0.01±0.24° vs. 0.01±0.26°, p=0.523) and for 45°LED vs. 45°RED (RW: -0.11±0.21° vs. 0.04±0.29°; LW: -0.08±0.21° vs. 0.10±0.26°) only a trend (p=0.050) was found.

/* Figure 5 about here */

DISCUSSION

This study was driven by the hypothesis that – as for line or rod adjustments and eye movements along either an earth-vertical or a body-longitudinal axis (Barnett-Cowan and Harris 2008; Haustein 1992; Tarnutzer et al. 2012) - graviceptive input is integrated when performing the LBT, regardless of the necessity of graviceptive input to solve this task. Due to the decrease of otolith effectiveness in roll-tilted positions (Schoene 1964; Tarnutzer et al. 2009a), we expected the accuracy and precision of the LBT to be reduced when roll-tilted. While we indeed observed a significant modulation of line bisection errors in the earth-horizontal paradigm (comparing 90°RED vs. 90° LED), these errors disappeared after correcting for the headward bias in the baseline earth-vertical (i.e., body-vertical) line bisection paradigm. The initially stated hypothesis therefore cannot be confirmed, since no evidence for graviceptive (otolithic) input being integrated for the line bisection task was found. This was true both when bisecting earth-horizontal and body-horizontal lines in different whole-body roll positions. Furthermore, we hypothesized that static roll-tilt over several minutes results in a post-tilt bias of the LBT, shifting bisections towards the previous roll-tilted position as described for the SVV (Day and Wade 1966; Tarnutzer et al. 2013). However, consistent with the lack of influence of gravity on errors while roll-tilted for the LBT, we did also not observe any post-tilt effect.

Instead, our results suggest that it is rather the orientation of the line relative to the subject's body-longitudinal axis that predicts the pattern of errors in the LBT than the orientation of the subject's body relative to gravity. Whenever the body-vertical axis and the line to bisect are in parallel, a headward bias seems to emerge, whereas for lines oriented perpendicularly to the body-longitudinal axis a leftward bias can be expected. This suggests that horizontal and vertical visual line bisections are independent tasks. Likewise, the increase of trial-to-trial variability in 90° ear-down positions with the line oriented parallel to the body-longitudinal axis can be explained by the higher variability when bisecting body-vertical lines compared to body-horizontal lines, as shown in upright position.

Impact of whole-body roll orientation on the LBT – comparison with previous studies

Regarding roll-angle dependent modulations in the visual LBT, previous research indicated a shift in earth-horizontal line bisection errors (relative to adjustments when upright) towards the direction of roll-tilt for 90°RED, while for 90°LED a slight shift in errors away from the direction of roll-tilt was observed for earth-horizontal lines with adjustment errors being significantly different between the two 90° roll-tilted positions (Bradshaw et al. 1985). While the bias towards the direction of roll-tilt at 90°RED could be explained by a headward bias in a body-vertical line bisection task, the footward bias described at 90° LED lacks a stringent explanation. For a body-horizontal line bisection task in the same study, a shift of bisection errors towards the direction of roll-tilt was noted for both 90° LED and 90° RED with adjustment errors being significantly different for the two roll-tilted positions. It should be noted, however, that differences between the paradigms applied by Bradshaw and colleagues (1985) and our experimental setup exist. Most importantly, Bradshaw required subjects to grasp and move a rod in such a way that a central fixation dot bisected the rod in two parts of equal length. Therefore, both the earth-fixed and the body-fixed paradigm required a coordinate-transformation since arm-in-space position was required to reach the rod in peripersonal space and to achieve the manipulation. In our paradigm, simple rotations of a knob in the body-fixed paradigm did not require such coordinate transformation. Noteworthy, trial-to-trial variability resulting from repetitive bisections as performed in our experimental paradigm may have shaded more subtle effects. Possibly, the trend towards significance for the corrected adjustments in paradigm 1 when comparing 45° RED and 45° LED would have become significant with additional data. However, errors of the LBT for 90° ear-down positions in paradigm were clearly overlapping (p=0.523).

Line bisections parallel to the body-longitudinal axis and in oblique orientation

For vertical lines a tendency to bisect above the objective center of the line (altitudinal neglect) has been noted (Bradshaw et al. 1985; Butter et al. 1989). McCourt investigated bisections of vertical and oblique lines using pre-bisected lines and concluded that errors in bisecting oblique lines does not result from the summation of pseudoneglect and altitudinal neglect (McCourt and Olafson 1997). According to this hypothesis, bisection errors should be greatest for diagonal lines from upper-left to lower-right. However, this was true only in their above/below (and not their left-right) decision context (McCourt and Olafson 1997). The authors explained these discrepancies by an independent system for vertical and horizontal stimuli. How distinct effects related to the independent systems for vertical and horizontal stimuli (McCourt and Olafson 1997) add up, therefore remains unclear. In our experiment, for the oblique (ULLR) condition, right- and downward errors were observed, while the oblique URLL condition was accurate. Regarding variability, the oblique conditions had larger variability, similar to the earth-vertical line bisection task.

Pseudoneglect and hysteresis in extrapersonal space

By demonstrating a significant effect of scanning direction both in upright and roll-tilted positions for the LBT, we did not only confirm previous observations of a scanning-direction effect when upright (Brodie and Pettigrew 1996; Chokron et al. 1998; Jewell and McCourt 2000) but also found that this effect is independent from the direction of gravity. These observations suggest an effect of hysteresis, which is the retardation of an effect when forces acting upon a body are changed (Merriam Webster definition). More specifically, hysteresis reflects the history-dependence of physical systems, as in our experimental setup, the initial position from which a desired (final position) is reached. Indeed the LBT is affected by recent history of hand activity when moving the cursor from the lateral (right or left) to a central position.

However, it is necessary to make the distinction between peripersonal space (within arm reach), where planning and execution of limb movements play a dominant role, and extrapersonal space (outside arm reach), where visual search and object recognition are more important. Far and near space are represented by functionally distinct neural circuits and are encoded in allocentric coordinates for extrapersonal space and probably represented in an egocentric system for peripersonal space (for a review see (Previc 1998)). Lines in near space are bisected to the left (McCourt and Jewell 1999; McCourt and Olafson 1997; Varnava et al. 2002), and noticeably, rightward errors have been observed when bisecting lines in extrapersonal space (Dellatolas et al. 1996; Longo and Lourenco 2006; Varnava et al. 2002). When using a stick to achieve the LBT this left-to-right shift disappeared (Berti and Frassinetti 2000; Gamberini et al. 2008), suggesting plasticity of space representations with tools like a stick expanding the near space (Longo and Lourenco 2006). Analogously, we observed left-side underestimation, although in our experiment the line was projected in the extrapersonal space (at 1.5m distance). Possibly, we virtually expanded peripersonal space by using a remote control. Varnava et al. (2002), who also used a tool (keyboard) in order to bisect a line at different distances, observed a rightward bias in extrapersonal space. Hence we must consider another reason why we observed pseudoneglect while bisecting lines in extrapersonal space. While our measurements took place in complete darkness, Varnava et al. (2002) describe a setting with the light on. Without visual distance cues in our setting, subjects may have perceived the line as closer, possibly explaining this discrepancy. The eminent role of object orientation relative to body orientation was also demonstrated in a study by Barbieri, showing that artificial walking patterns could be identified more easily when aligned with an egocentric reference (Barbieri et al. 2013).

A leftward bias has also been observed for the assumed direction of illumination in shaded images (Howard et al. 1990) (Jenkin et al. 2003; Jenkin et al. 2004; McManus et al. 2004) and it has been demonstrated, that this leftward bias persists when tilted in the roll plane (Barnett-Cowan et al. 2013; Jenkin et al. 2003). Likewise, leftward biases were reported for spatial perception of the body

(Barnett-Cowan and Harris 2008; Barnett-Cowan et al. 2013; Tarnutzer et al. 2012), perceived direction of gravity (Schuler et al. 2010) and the perceptual upright (Dyde et al. 2006). This leftward bias is likely attributable to a bias in the representation of the body and was linked to pseudoneglect as well (Barnett-Cowan et al. 2013). In our experimental paradigms, we observed a slight leftward bias when bisecting lines oriented along the body-horizontal axis, both when upright and when roll-tilted. Whether pseudoneglect in the visual LBT is linked to a biased representation of the body as well or rather a consequence unilateral hemispheric activation (Bowers and Heilman 1980; Bradshaw et al. 1987), scanning tendency due to reading habits (Chokron and De Agostini 1995; Chokron and Imbert 1993) or cursor movements (Chokron et al. 1998), however, remains to be determined in future studies.

CONCLUSIONS

Unlike for visual line adjustments performed either along earth-or body-fixed frames of reference; we did not observe a modulatory effect of gravity on visual line bisections. Most likely, this is because with our setup subjects performed the visual LBT in an egocentric reference frame and no shift to an earth-fixed frame of reference that may have triggered the integration of graviceptive input to the LBT was required. The previously described shifts in the LBT when roll-tilted 90° ear-down therefore can only be partially explained with our data set, leaving shifts away from the side of roll-tilt (as described by Bradshaw and colleagues for 90° LED (Bradshaw et al. 1985)) open to discussion. Of importance for future studies, researches should take into account and control for changing relative orientations of the visual line to and the subject in the roll plane will influence the pattern of bisection errors.

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FIGURE LEGENDS

Figure 1

For this study, a motorized turntable that allowed positioning of the subjects in any roll-tilted position and projecting a luminous line (earth-horizontal in this case) was used, as illustrated in panel A. The experimental paradigms are explained in panel B: while both for paradigm 1 (earth-horizontal line) and for paradigm 2 (body-horizontal line) baseline recordings in upright position were obtained first, this was followed by repetitive visual line bisections in a static whole-body roll-tilted position (±45° or ±90°) and immediately after returning upright by another series of line bisections in upright position. In each position measurements were obtained during 5min. For each condition, inlets illustrate both the subject's whole body roll orientation relative to gravity and the orientation of the line relative to the subject (including a short perpendicular line that is used to divide the line in two parts of equal length).

Figure 2

Line bisection errors (filled circles) relative to the objective center of the line (dotted horizontal line) are plotted against time in a single subject (C.M.) at baseline (panel C), while roll-tilted (trials interconnected with a grey line) and upon return to upright (trials interconnected with a black line) (panels ABDE) for the earth-fixed line paradigm. For 90° ear-down positions a clear shift of adjustments towards the whole-body roll position can be seen during the roll-tilt period. A description of the insets can be found in the legend to figure 1.

Figure 3

Average (±1SD) line bisection errors for right-handed subjects (n=20) are plotted as a function of whole-body roll position (upright, ±45°, and ±90°) for the earth-fixed line paradigm (panel A) and for the body-fixed line paradigm (panel C). In panels B (earth-fixed line paradigm) and D (body-fixed line paradigm) trial-to-trial variability (±1SD) is plotted against whole-body roll position.

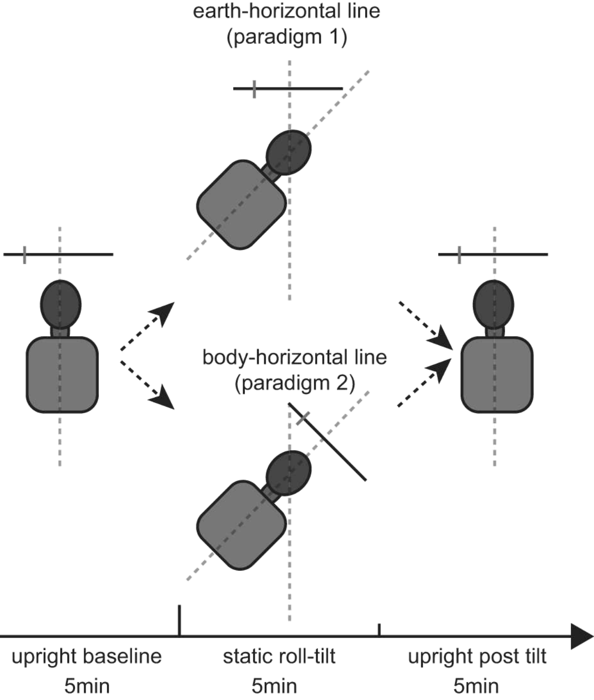
Line bisection errors are plotted separately for rightward (grey circles interconnected with a grey solid line) and leftward (black squares interconnected with a black dashed line) cursor movements. A description of the insets can be found in the legend to figure 1.

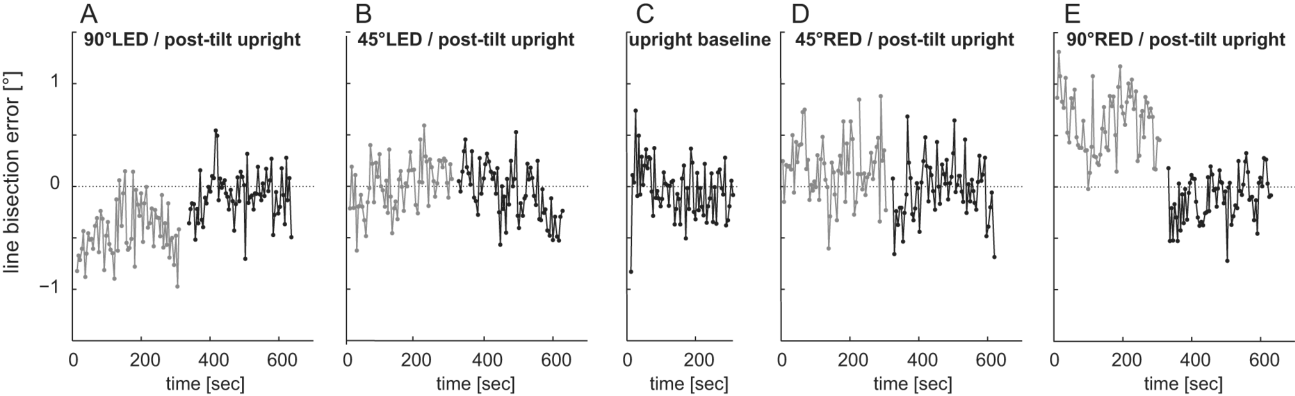
Figure 4

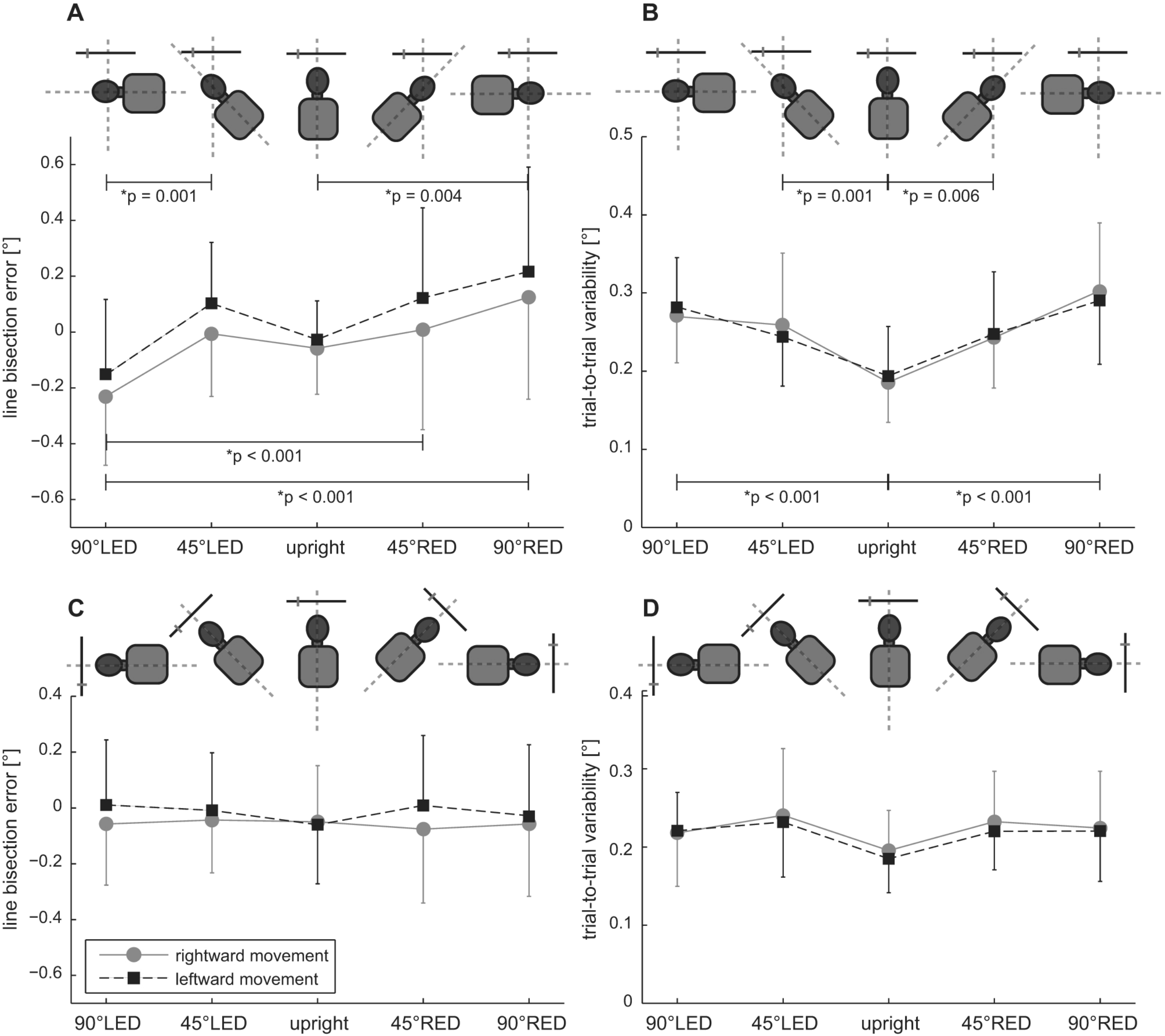
Average (±1SD) line bisection errors (panel A) and variability (panel B) are plotted for horizontal, vertical, upper-left-to-lower-right oblique (ULLR) and upper-right-to-lower-left oblique (URLL) lines for the control group (n=17; missing data in 3 subjects). Line bisection errors are again plotted separately for rightward (grey circles) and leftward (black squares) cursor movements. A description of the insets can be found in the legend to figure 1.

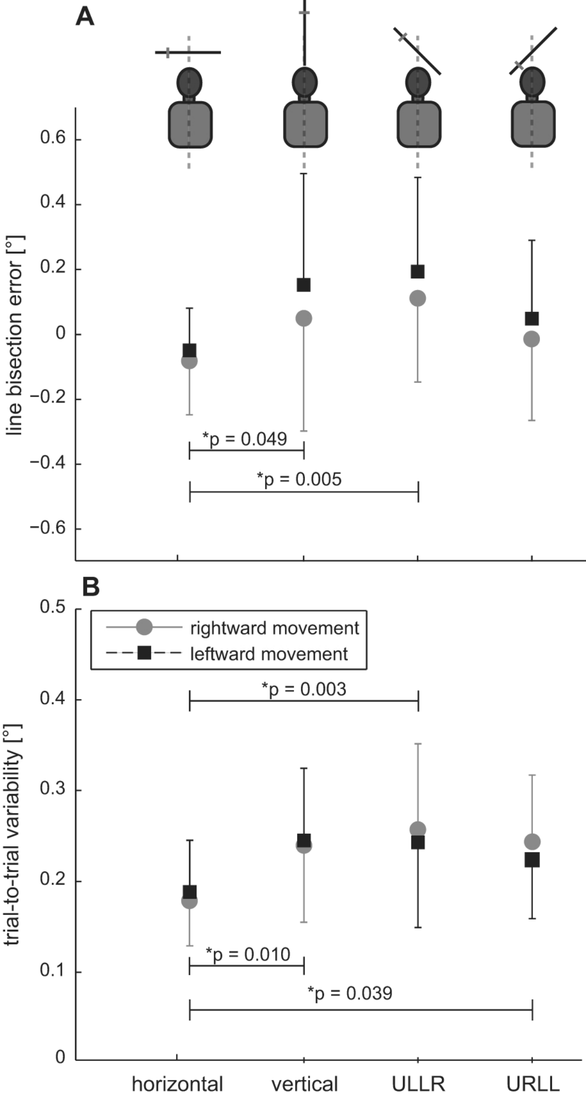
Figure 5

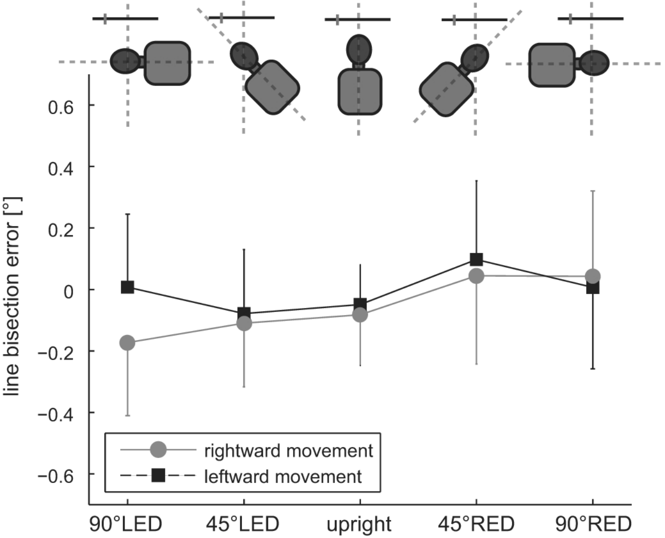
Line bisection errors from paradigm 1 (earth-fixed paradigm) after correcting for bisection errors while upright according to the line orientation relative to body-longitudinal axis. Average (±1SD) line bisection errors are plotted as a function of whole-body roll position (upright, ±45°, and ±90°). Again, line bisection adjustments are plotted separately for rightward (grey circles interconnected with a grey solid line) and leftward (black squares interconnected with a black dashed line) cursor movements. A description of the insets can be found in the legend to figure 1.


earth-horizontal line
(paradigm 1)
body-horizontal line
(paradigm 2)
upright baseline
5min
static roll-tilt
5min
upright post tilt
5min


A
90°LED / post-tilt upright
B
45°LED / post-tilt upright
C
upright baseline
D
45°RED / post-tilt upright
E
90°RED / post-tilt upright
line bisection error [°]
1
0
−1
0
200
400
600
time [sec]


A
B
C
D
line bisection error [°]
trial-to-trial variability [°]
*p = 0.001
*p = 0.004
*p < 0.001
*p < 0.001
*p = 0.001
*p = 0.006
*p < 0.001
*p < 0.001
90°LED
45°LED
upright
45°RED
90°RED
rightward movement
leftward movement


A
B
line bisection error [°]
0.6
0.4
0.2
0
−0.2
−0.4
−0.6
*p = 0.049
*p = 0.005
trial-to-trial variability [°]
0.5
0.4
0.3
0.2
0.1
0
rightward movement
leftward movement
*p = 0.003
*p = 0.010
*p = 0.039
horizontal
vertical
ULLR
URLL


0.6
0.4
0.2
0
−0.2
−0.4
−0.6
line bisection error [°]
rightward movement
leftward movement
90°LED
45°LED
upright
45°RED
90°RED